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Foraging at the edge of the world: low-altitude, high-speed manoeuvering in barn swallows

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While prior studies of swallow manoeuvering have focused on slow-speed flight and obstacle avoidance in still air, swallows survive by foraging at high speeds in windy environments. Recent advances in field-portable, high-speed video systems, coupled with precise anemometry, permit measures of high-speed aerial performance of birds in a natural state. We undertook the present study to test: (i) the manner in which barn swallows (*Hirundo rustica*) may exploit wind dynamics and ground effect while foraging and (ii) the relative importance of flapping versus gliding for accomplishing high-speed manoeuvers. Using multi-camera videography synchronized with wind-velocity measurements, we tracked coursing manoeuvers in pursuit of prey. Wind speed averaged 1.3–2.0 m s^{-1} across the atmospheric boundary layer, exhibiting a shear gradient greater than expected, with instantaneous speeds of 0.02–6.1 m s^{-1}. While barn swallows tended to flap throughout turns, they exhibited reduced wingbeat frequency, relying on glides and partial bounds during maximal manoeuvers. Further, the birds capitalized on the near-earth wind speed gradient to gain kinetic and potential energy during both flapping and gliding turns; providing evidence that such behaviour is not limited to large, fixed-wing soaring seabirds and that exploitation of wind gradients by small aerial insectivores may be a significant aspect of their aeroecology.

This article is part of the themed issue 'Moving in a moving medium: new perspectives on flight'.

1. Introduction

As evidenced by the diversity of volant species, flight is an effective means of locomotion. While the physiological investment is large [1], the return is high speed and extremely low cost of transport. Further distinguishing it from terrestrial locomotion is that the locomotor substrate routinely offers exploitable energy, as air is set in motion by differential heating. While there may exist unusual microclimates where flying animals experience only still air (e.g. laboratories), the vast majority of flying takes place in air that is moving—as wind, thermals, deflections or functionally random turbulence (table 1).

As a subdiscipline of aeroecology [2], the effects of the aerial environment upon animal flight is understudied because of technical challenges. Recent evidence using accelerometry and GPS loggers reveals European shags (*Phalacrocorax aristotelis*) modulate their flight behaviour in response to variable wind probably to minimize energetic costs during take-off and cruising flight [3]. Larger birds also make extensive use of fixed, full-wing postures to exploit energy from their

Table 1. Nomenclatures.

g	gravitational acceleration
m	mass
u, v, w	wind velocity in X, Y and Z directions
$\bar{u}$, $\bar{v}$, $\bar{w}$	mean velocity in the X, Y and Z directions
KE_{grnd}	kinetic energy relative to ground
KE_{air}	kinetic energy relative to air
PE	potential energy
TE_{grnd}	total energy relative to ground
TE_{air}	total energy relative to air
Ti_u, Ti_v, Ti_w	turbulence in X, Y and Z directions
U_{air}	air speed
U_{body}	speed of body
U_{grnd}	ground speed
WBF	wingbeat frequency
X, Y, Z	position along forward, lateral and vertical axes in global frame of reference
Z_r	reference location on Z-axis
σ_u, σ_v, σ_w	standard deviation of velocity in X, Y and Z directions
α	exponent

aerial environment, using thermal (e.g. vultures, *Cathartidae*) or dynamic soaring (e.g. petrels and albatrosses, *Procellariiformes*) to minimize the cost of transport [4–7]. Further, birds are routinely observed using the energy of orographic updrafts [8], placing them in close proximity to the terrestrial environment that provides the updraft, which requires precise manoeuvering and speed control to effectively capture the energy while avoiding the deflecting structure. Deft manoeuvering is also required to exploit near-ground wind gradients: i.e. a bird ascending from still air through a gradient of increasing wind velocity can increase its airspeed, providing a gain in kinetic and/or potential energy. Here again, precise body position and situational awareness (height, wind direction and magnitude, obstacles) are required of the animal. The atmospheric boundary layer is characterized by shear layers with average horizontal velocity logarithmically increasing with height above the ground or water from zero at the surface (due to the no-slip condition) to free-stream velocity 1–2 km above the Earth [5,9,10]. Because of this, a diverse array of birds in cruising flight will position themselves closer to the water or ground surface, within a region of reduced velocity, when flying into a headwind compared with a tailwind [11]. Flight immediately adjacent to the surface may also permit them to exploit ground effect [12], the reflection of downwash and tip vortices near the ground, which reduces induced drag.

Most small birds, owing to their low inertia relative to the drag created by their wing surface area, spend much less time in the fixed-wing gliding posture [13]. Swallows (Hirundinidae) are a dramatic exception; although they possess perhaps the largest wings relative to their body mass among birds [14], they are known for spending considerable time gliding [15], particularly when foraging [16]. In addition, barn swallows (*Hirundo rustica*) have long been noted for their low-altitude foraging [14,17], placing them in proximity to such near-earth wind gradients. Here we test whether the flight of barn swallows is influenced by wind velocity within this shear layer. Previous research into the kinematics of free-flight manoeuvering in swallows has been conducted in relatively still air to avoid uncertainties imposed by wind dynamics [18–20]. However, we hypothesize these dynamics represent a source of useful environmental energy and exert selective forces upon flight morphology and behaviour in windy environments.

Swallows are thought to be among the most manoeuverable species of birds, and barn swallows in particular may be ideally suited to exploiting near-earth gradients. Foraging on aerial insects, many highly manoeuverable in their own right, has undoubtedly imposed key selective pressures on their evolution, resulting in exceptionally low wing loading, and exceptionally large tails that may function both as aeroelastic devices [21] as well as sexually selected signals [18,22]. In theory, these features may also allow them to more effectively extract energy from wind gradients [5]. Because instances of near-earth gradients and foraging manoeuvering are inextricably linked in this species, our second goal is to examine the turning manoeuvering performance of barn swallows, particularly within the context of fixed-wing versus flapping wing manoeuvering. Low wing (and perhaps, tail) loading confers high manoeuverability (small turn radius) without the need to slow and flap through a turn, and has thus been used as a defining characteristic in ecomorphological treatments of flight [23,24]. Fixed-wing manoeuvering requires much less metabolic power than flapping [25,26]. However, all birds flap to some degree, and birds that can effect a small-radius turn while gliding versus those that must slow and flap through the same turn lie on a continuum. Species that can manoeuver with fixed wings have been described as intrinsically manoeuverable *versus* those that must always flap as facultatively manoeuverable [14,27,28]. New research on tandem flights in cliff swallows (*Petrochelidon pyrrhonota*) reveals that cliff swallows turn with facultative flapping rather than gliding [20]. However, it is not clear where on this continuum barn swallows lie, and, thus, to what degree their flight and aeroecology can be described by fixed-wing parameters such as wing loading.

2. Material and methods

(a) Kinematics

We recorded the kinematics of swallows using high-speed videography. We used five synchronized high-speed cameras (3× NR5 and 2× N5S1, Integrated Design Tools, Inc., Tallahassee, FL, USA; recording 2336 × 1728 pixel images at 100 Hz). Each camera was equipped with a 24 mm lens (Nikon 24 mm f/2.8 AI-s, Nikon USA). The cameras were placed in an arc with a maximum inter-camera distance of approximately 11 m (figure 1*a*) and calibrated using a structure from motion approach [29]; the reference object had a length of 1.47 m. The origin of each calibrated space was placed at our ultrasonic anemometer (see below) and aligned with $+X$ pointing magnetic North and $+Z$ pointing upward by using the shaft of the sensor (placed in the horizontal) and gravitational acceleration (global vertical) measured from the kinematics of a falling ball.

This arrangement produced a measurement volume approximately 8200 m^3 seen by two or more of the five cameras and within a range set by the distance to the furthest bird analysed. The median re-projection error for the bird points was 1.2 pixels,

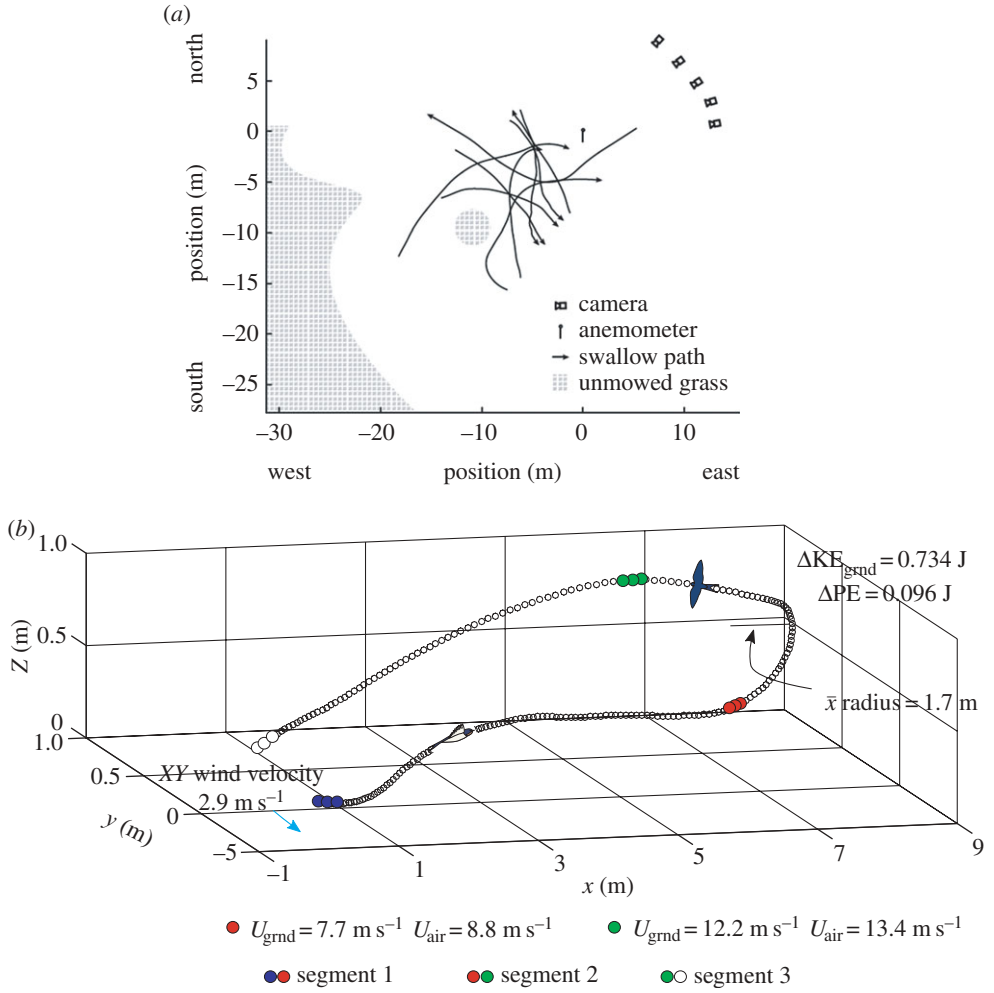

Figure 1. Camera placement and example of flight path for a barn swallow. (*a*) Overhead view of typical recording layout showing the position of the high-speed video cameras, the ultrasonic anemometer and swallow flight paths while foraging over a field located at sea level at The Oregon Institute of Marine Biology, Coos Bay, OR, USA. The flight paths begin and end according to either the recording duration limits of the cameras or the edges of the volume seen by two or more cameras. Flights were over mowed grass approximately 8 cm in height with some unmowed regions >1 m in height (electronic supplementary material, figure S4). (*b*) Flight path and dynamics of a swallow in an approximately 180° turn. The flight path was initially perpendicular to the wind; at the beginning of the turn (segment 2) the bird began to turn into the wind. The initial groundspeed (U_{grnd}) and airspeed (U_{air}) were taken as the mean of the first three values for the segment. In this turn, from the beginning to the end (green markers) the bird does not flap, yet it increases speed and altitude, and, hence, kinetic and potential energy (electronic supplementary material, figure S1).

which corresponded to a median [*X*, *Y*, *Z*] 95% CI width of [1.0, 1.0, 0.3] cm and a three-dimensional confidence interval width of 1.7 cm.

We digitized wing and body kinematics in a subsample of 42 of 120 foraging flights that were recorded in digital video, all of which had synchronized measurements of wind velocity and which provided the most accurate kinematic assessment of flight paths during manoeuvers. Tracks of body position were smoothed to these 95% confidence intervals using a smoothing spline and the first and second derivatives with respect to time calculated from the spline polynomials. These inputs were used to calculate metrics including radius of curvature, centripetal force, and mass-specific kinetic and potential energy [30].

We measured use of intermittent non-flapping phases (gliding or partial-bounding; [15]) using visual sampling of the video and report effective wingbeat frequencies that include these non-flapping phases.

(b) Flight sampling and animal identification

We recorded 120 flights over five days from 10 to 14 June 2014. The birds in these flights were from a colony of approximately 20 nesting in the outdoor-tank rooms at the Oregon Institute of Marine Biology, Charleston, Coos Bay, OR, USA. Birds were captured using hand-held mist nets, weighed using a digital scale and digitally photographed with their right wings fully spread. Tails were spread to random angles between 45° and 90° and photographed; wing span, area and maximum continuous width [31] were measured using ImageJ (table 2). We placed coded ID tags (Lotek, Ontario, CA NTQB-1, featuring a 1 s burst rate; 0.29 g) on 10 birds (5 males, 5 females). Birds were released at the site of capture, and their release flights recorded using high-speed videography as described above. Tags were recorded using a Lotek radio receiver (receiver model SRX-DL-1) connected to a three-element folding yagi 9164–168 MHz (model F166-3FB) and 150–170 MHz Whip Antenna (model SLA/Ft-2). We obtained at least one flight from six tagged birds (mean number = 8 ± 8, range 1–21). Anonymous flights were 71 of 120, or 59%. We digitized 42 (35%) of the total recorded flights. Among these 42 digitized flights, 10 flights (34%) were from four of the tagged birds (range 1–5 flights digitized per bird). Ultrasonic anemometer data were missing from two flights (but available for all of the 42 digitized flights analysed here), so we report wind velocity data concurrent with 118 flights recorded using video.

(c) Flight analyses

Individual flights were categorized as straight (heading change < 20°) and turning (heading change > 20°). Turning flights were

Table 2. Barn swallow morphometrics means ± s.d. (range).

mass (g)	wing span (cm)	wing loading (Pa)	aspect ratio	MCW at 90° (cm)
16.7 ± 0.1 (18.5–15.5)	29.0 ± 0.1 (30.5–27.4)	14.1 ± 1.0 (16.2–12.6)	7.3 ± 0.3 (7.9–6.9)	9.6 ± 0.39[a]

[a] S.d. of estimate, regression of maximum continuous width by angle of tail spread; width = 1.102 + angle (0.095); $R^2 = 0.88$; $n = 31$.

each further divided into three segments defined by the turn itself: before = segment 1, during = segment 2 and after = segment 3 (figure 1*b*). Not all flights had all segments, and five flights had more than one turn. One flight was further subdivided for analysis due to a vertical manoeuver during the turn (pitch-up). The during-turn segment 2 was defined by establishing the midpoint in heading change, finding the minimum radius of curvature and defining the turn as the portion of the flight where the turn radius < 3× minimum radius. Ground speed (U_{grnd}) was calculated using change (Δ) in *XYZ* position as a function of time in the ground-reference frame. To estimate airspeed (U_{air}), the *X* and *Y* components of wind velocity (*u* and *v*, respectively) were added to the Δ*X* and Δ*Y* component of ground position, and airspeed was calculated using these adjusted values. Because of the proximity of the flights to the anemometers (less than 10 m), the birds were subjected to *u* and *v* wind velocities close to those measured; however, the inherently smaller and more variable Z wind velocities (*w*) were not incorporated into airspeed calculations (see Aeroecology section as follows).

Full-segment means were calculated for each turn segment. To measure changes in speed and height between segments, we used initial values (a mean of the first three values for the segment) for air and ground speeds, height and heading for each segment (e.g. change in ground speed for segment 1 = segment 2 initial – segment 1 initial; figure 1*b*) Height changes observed during some recorded manoeuvers meant that the birds passed through the steep near-ground wind gradient, and thereby might be able to exploit the energy of that gradient. To assess the possible effect of the wind gradient on these flights, we characterized segment 2 of the turns using the swallow's ground-track direction relative to the wind. Upwind turns were those where the average wind direction through segment 2 was a headwind; conversely, during downwind turns, the average wind direction for segment 2 was a tailwind. Flights were further categorized as upwind, downwind and crosswind for straight flights (angle to wind between 75° and 105°) to examine differences in flight behaviours with respect to the local aerial environment. Changes in kinetic energy ($KE = \frac{1}{2} mU^2_{body}$), potential energy ($PE = mgZ$) and total energy (TE) were calculated for each segment across these turn conditions, with the mass ($m = 0.0166$ kg) of the bird taken from the average of the measured birds. When foraging in close proximity to the ground, the birds need to account for the work they must to do to the air as well as the work they must do (or avoid doing) relative to the ground (given that their prey are largely ground-based, and that a collision with the terrestrial environment at 10 m s^{-1} would be catastrophic), KE was calculated in both ground ($\frac{1}{2} mU^2_{grnd}$) and air ($\frac{1}{2} mU^2_{air}$) reference frames.

(d) Aeroecology

During recorded flights, average temperature was 16 ± 2°C. The site was at sea level, with average air density = 1.23 kg m^{-3}.

We measured wind velocity using an ultrasonic anemometer placed at a height of 0.35 ± 0.01 m and a vane anemometer at a height of 3.05 ± 0.05 m; the horizontal distance between the two devices was 9.7 ± 3.3 m. The ultrasonic anemometer was a V-style three-axis design (Applied Technologies, Inc.) with 10-cm path length between probe sensors and probe array dimensions 17.8 × 17.8 × 17.8 cm. Nominal accuracies were ±0.01 m s^{-1} for wind speed and ±0.1° for wind direction. We recorded wind velocity to a laptop computer via an RS-232C connection, sampling at 20 Hz using a custom MATLAB script. Our rotating vane, digital anemometer (DA400 meter with DA40 impeller-style probe; Pacer Instruments) had a resolution of 0.01 m s^{-1} and a nominal accuracy of ±1% of reading. Readouts were averaged over 2-s intervals. The probe was coupled to a 40-cm wind vane with a freely rotating base. We used visual inspection of the vane anemometer orientation to measure wind direction relative to magnetic north.

Immediately after the end-triggering of a video recording, one observer recorded wind velocity displayed by the wind-vane anemometer. This same observer then stopped the ultrasonic anemometer recording. The clocks of the camera and ultrasonic anemometer controlling computers were synchronized, allowing near-instantaneous correspondence (1-s resolution) between low height wind conditions at the time of the flight recording. Owing to variance in observer reaction time, temporal uncertainty of our measure of wind velocity at 3 m in height, and vertical wind gradient, was approximately 5 s.

To characterize the gradient at the sampling location, we obtained a vertical transect of three-dimensional wind velocities from 0.35 m to 3.18 m above the ground, using the ultrasonic anemometer sampling for 5 min at average 21 ± 4 cm intervals for heights ≤ 1 m and 54 ± 8 cm intervals for heights > 1 m. We fitted a log-normal curve to the mean horizontal wind speeds as a function of height above the ground [9] to validate our interpolation of wind speed within the near-ground atmospheric boundary layer. Based on the log-normal best fit of the vertical transect data, we derived a natural-logarithmic regressions to interpolate wind speed at heights between the ultrasonic and vane anemometers at the time of the flight.

Summary statistics of horizontal and vertical wind speed (mean ± s.d.) and horizontal direction (circular mean ± circular standard deviation) were calculated, the latter using CircStat, a MATLAB Toolbox for Circular Statistics [32]. We used least-squares regression to summarize the correlation between horizontal wind speeds measured using the ultrasonic and vane anemometer.

Finally, we calculated turbulence intensity (Ti) using the ultrasonic anemometer data for velocities *u*, *v* and *w* sampled in the *X*, *Y* and *Z* directions [32]:

$$\mathrm{Ti}_u = \frac{\sigma_u}{\bar{u}}, \quad \mathrm{Ti}_v = \frac{\sigma_v}{\bar{v}} \quad \text{and} \quad \mathrm{Ti}_w = \frac{\sigma_w}{\bar{w}}, \tag{2.1}$$

where σ is the standard deviation of the flow; σ_i, is standard deviation and $\bar{i}$ is mean velocity in a given direction. We used autocorrelation to calculate the length scale in each axis by plotting an autocorrelation function ('acf' MATLAB script written by Calvin Price) of the flow with respect to time lag, summing the area under the autocorrelation curve up to the point where the curve became 0, and multiplying this area by $\bar{i}$ for a given direction [33].

3. Results

(a) Aeroecology

The barn swallows flew in a windy environment that, on average, was relatively predictable, although instantaneous wind velocities were highly variable (20 Hz sampling; figure 2*a*,*b*).

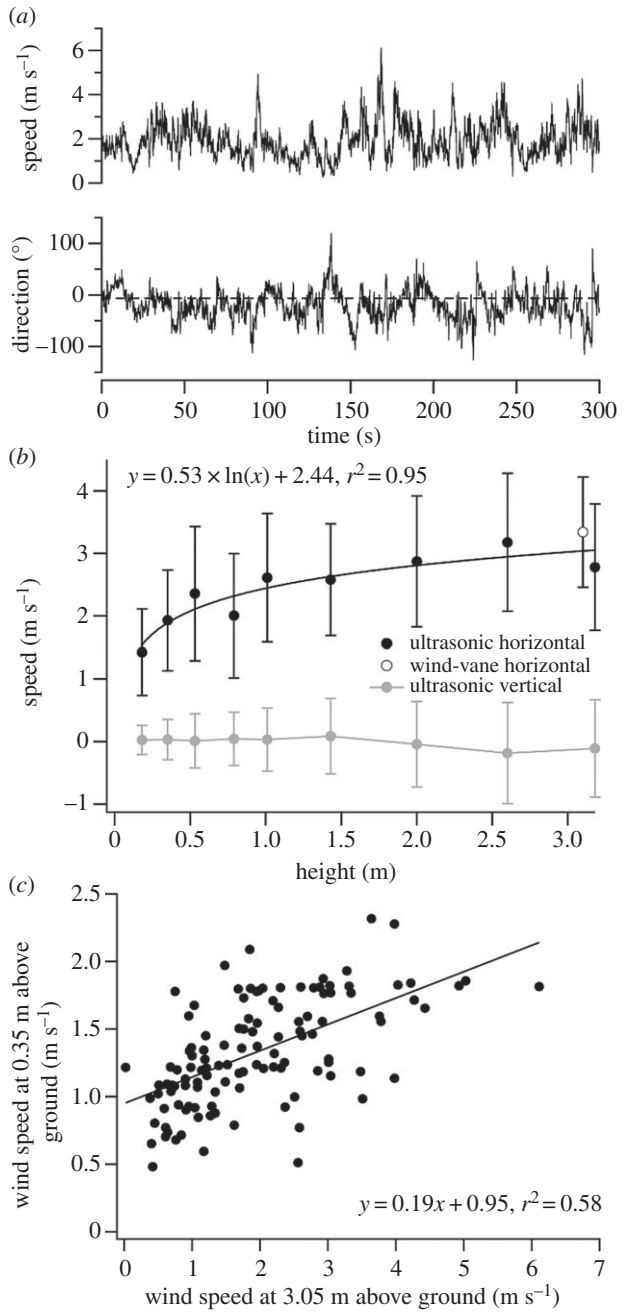

Figure 2. Wind velocities during measurements of flight in barn swallows. (*a*) Instantaneous speed (upper panel) and direction (lower panel) during 5-min ultrasonic anemometer reading with height = 0.35 m. Dashed line indicates average wind direction measured using vane anemometer with height = 3.05 m. (*b*) Average speed (±s.d.) during 5-min samples (black filled circles = ultrasonic anemometer horizontal (*uv*) resultant; grey, vertical (*w*); open circle, wind-vane anemometer). Fitted curve, natural-logarithmic regression. (*c*) Wind speeds measured during barn swallow flights using ultrasonic anemometer at height of 0.35 m relative to speeds measured using wind-vane anemometer at height of 3.05 m. Least-squares regression line, $n = 118$.

Along a vertical transect, average wind speed measured using the ultrasonic anemometer increased from 1.42 ± 0.69 m s^{-1} at 0.18 m height to 3.17 ± 1.10 m s^{-1} at 2.6 m height (figure 2*b*). The value at 3.18 m was 2.78 ± 1.01 m s^{-1}, similar to the average value of 3.34 ± 0.88 m s^{-1} measured using the vane anemometer at 3.05 m height. Instantaneous sampling at 0.35 m height revealed a range of wind speed from 0.26 to 6.14 m s^{-1}, and variation in wind direction (relative to magnetic north: approx. 0°) was from −126 to +120° (figure 3*a*).

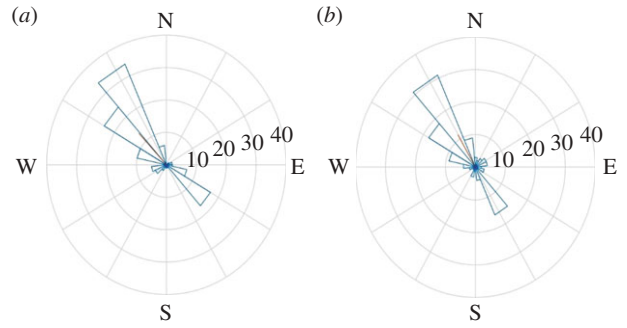

Figure 3. Histograms of incoming direction of wind during barn swallow foraging flights ($n = 118$) with data from (*a*) ultrasonic anemometer at height of 0.35 m and (*b*) wind-vane anemometer at height of 3.05 m. Inset numbers indicate frequency of observations. (Online version in colour.)

For this same time interval, the vane anemometer indicated a wind direction of −12° at 3.05 m (figure 3*b*). The horizontal (*xy*) components of wind velocity dominated; vertical (*z*) velocity in this transect averaged -0.01 ± 0.09 m s^{-1} among transect heights. Variation in vertical velocity increased with height above the ground (figure 2*b*). Near the average heights of bird flight (i.e. approximately 0.43 m), mean vertical velocity was $0.04 + 0.43$ m s^{-1} at 35 cm and 0.01 ± 0.43 m s^{-1} at 53 cm (figure 2*b*). On three of the four days of recordings, the wind was predominantly from the north northwest, and on one day, it was from the south southeast (figure 5). Over all recordings, average wind direction at 0.35 m height was 343 ± 78° (circular s.d.) and 331 ± 81° at 3.05 m.

The speed gradient was slightly steeper than is typically assumed [9]. Power-law relationships for wind speed are described by $U_{\mathrm{wind}}/U_{\mathrm{r}} = (Z/Z_{\mathrm{r}})^{\alpha}$, where U_{wind} is wind speed at height Z and U_{r} is known wind speed at reference height Z_{r}. The exponent, α, is frequently assumed to be 0.143. The exponent calculated from our vertical transect was 0.24. A natural-logarithmic regression [9] fit the data well ($y = 0.53\ \ln(x) + 2.44$; $r = 0.95$; figure 2*b*). On four occasions, we lacked vane anemometer data due to timing difficulties, and the wind at bird height Z was estimated using average values from the two anemometers taken at the time of the flights. The average wind gradient for all flights was described by speed (m s^{-1}) = 0.67 ln(height) + 2.07. The average height at which speed was estimated by this equation to be 0 m s^{-1} was 0.047 m, in agreement with the value of 0.05 m assumed by Ruggles [9].

In our vertical transect, turbulence in the horizontal plane was of greater magnitude than that in the vertical direction. Averaged among sample heights, Ti_u was 38 ± 7% (range 30–53%), Ti_v was 42 ± 8% (36–59%) and Ti_w was 17 ± 3% (14–22%). Length scales for turbulence in the horizontal plane were much greater than the wingspan of the swallows. For example, at 0.35 m in height, the length scales were 3.9 and 1.5 m. These corresponded to time scales of 13.4 and 5.3 s, respectively. By contrast, length scale for vertical turbulence at 0.006 m was much smaller than the wingspan, yielding a time scale of 0.02 s.

Average U_{wind} measured during all recorded flights using the ultrasonic anemometer at 0.35 m height was 1.33 ± 0.39 m s^{-1} (range 0.48–2.32 m s^{-1}) and $1.97 + 1.17$ m s^{-1} (range 0.02–6.11 m s^{-1}) measured at 3.05 m height using the vane anemometer. A linear relationship existed between U_{wind} measured at the two heights, but considerable scatter was evident about the regression line (figure 3*c*).

Table 3. Overall means ± s.d. (range).

U_{grnd} (m s^{-1})	U_{air} (m s^{-1})	height (m)	duration of flight (s)	WBF (Hz)
9.3 ± 2.4 (19.4–5.2)	9.5 ± 2.7 (19.4–3.7)	0.43 ± 0.78 (4.1 to −1.6)	2.0 ± 0.8 (4.0–0.4)	6.6 ± 3.2 (14.6)

Table 4. Overall means turning flight (segment 2).

	n	mean	s.d.	max	min
WBF (Hz)	38	6.7	3.6	14.6	0.0
mean radius (m)	37	5.1	3.0	15.2	1.0
peak (g)	37	4.4	1.4	7.8	2.1
mean (g)	37	3.3	1.2	6.5	1.8
entire segment mean U_{grnd} (m s^{-1})	38	8.7	1.5	12.8	5.4
entire segment mean U_{air} (m s^{-1})	38	9.0	2.1	14.7	6.0
turn duration (s)	37	0.6	0.3	1.5	0.2
Δheight (m)	38	0.5	0.7	2.9	−0.7
heading change	38	109.7	84.0	291.4	19.6
turn rate (deg s^{-1})	38	209.5	194.0	715.5	25.6

Pertaining to the relevance of the recorded wind data to the observed flight dynamics, the average bird height was 0.43 ± 0.78 m (versus 0.35 m for the ultrasonic anemometer), and the average horizontal distance of the bird to the ultrasonic anemometer was 10.3 ± 5.5 m.

(b) Flights

(i) Overall

Of the 42 digitized flights, 10 were straight flights (change in heading < 20°), and 32 were turning flights (table 3). Mean duration of measured flight was 1.99 ± 0.79 s (0.43–4.0 s). Mean flight speeds (U_{air} = 9.5 ± 2.7 m s^{-1} (range 19.4–3.7 m s^{-1}); U_{grnd} = 9.3 ± 2.4 m s^{-1} (19.4–5.2 m s^{-1}) and altitudes (height (Z) = 0.43 ± 0.78 m; max = 4.1 m) were consistent with other reported values for foraging barn swallows [14,17] and wind tunnel studies [34]. Given how dynamic most of the flights were, mean values represent little but provide a sense of scale; succinctly, the recorded flights were very low and very fast. Overall, the airspeeds were above theoretical minimum power speeds (6.7 m s^{-1}; [35]), and below the theoretical minimum cost of transport speed (13.2 m s^{-1}; [35]). The birds were at times low enough (less than one wingspan, approximately 0.3 m) to probably benefit from the lower induced drag of ground effect [12], but overall spent little time at these heights. While the average height of the flights of (0.43 m) was very low, the variability in ground height in even our relatively flat flight sampling location made quantifying their precise height above ground difficult. Taking only those flights (n = 10) within 6.5 m (mean = 5.4 m) of the ultrasonic anemometer (for which we are certain of the ground height, as it served as the origin of the calibrated space), for only one flight (duration 1.3 s) was the mean height of the flight below 0.3 m.

Mean wingbeat frequency (WBF, number of wingbeats recorded over the duration of the entire flight, including intermittent non-flapping phases) was 6.6 ± 3.2 Hz.

(ii) Coursing: straight flights and segment 1

We recorded only 10 flights that lacked a turning manoeuver of less than 20° of heading change. To further examine the coursing behaviour from which manoeuvers are initiated, we included straight portions of the turning flights (segment 1) that did not feature rapid pitch-up manoeuvers typical of prey capture (electronic supplementary material, table S1). Comparison of upwind, downwind and crosswind flights, indicated that segment 1 groundspeed (e.g. U_{grnd}, figure 1*b*) of upwind flying birds was somewhat lower (9.4 ± 1.6 m s^{-1}) than that of birds flying downwind (10.2 ± 1.7 m s^{-1}), while crosswind flights were intermediate (9.3 ± 1.7 m s^{-1}; ANOVA p = 0.08). Similarly, no statistical differences in segment 1 mean airspeeds (U_{air}) for downwind, upwind and crosswind flights were observed (9.7 ± 1.7 m s^{-1}; 10.3 ± 2.2 m s^{-1} and 8.8 ± 1.1 m s^{-1}, respectively; p = 0.25 Kruskal–Wallis ANOVA); nor did WBF differ (6.8 ± 2.2 Hz; 6.5 ± 2.9 Hz and 5.6 ± 3.0 Hz, respectively; p = 0.62).

Discarding the crosswind category, we examined the average TE changes during downwind and upwind straight flights as a measure of inherent variability (using segments 1 and 2 initial flight speeds). In doing so, we found no significant differences in means (e.g. ΔTE_{grnd} = 0.0 ± 0.4 J downwind versus −0.2 ± 0.5 J upwind; p = 0.57; electronic supplementary material, table S2) or correlation in energy change with wind speed (e.g. upwind ΔTE_{grnd} by wind speed R^2 = 0.00; p = 0.92; downwind ΔTE_{grnd} by wind speed R^2 = 0.00; p = 0.50; electronic supplementary material, table S2).

(iii) Turning flights

The remaining 32 flights included six flights with more than one manoeuver, for a total of 38 manoeuvers. Turning flights were highly variable in radius (mean 5.1 ± 3.0 m; range 15.2–1.0 m) and turn rate (mean = 209.5 ± 194.0 deg s^{-1}; range: 715.5–25.6 deg s^{-1}), and frequently involved simultaneous changes in height (mean ΔZ = 0.5 ± 0.7 m; range: 2.9–0.7 m; table 4). While all turning manoeuvers were

Table 5. Turning flights (segment 2).

	mean ± s.d. within segment changes			regression: changes by wind speed[a]	
	down ($n = 19$)	upwind ($n = 19$)	$p^{(test)}$	down ($n = 19$)	upwind ($n = 19$)
Δheight (m)	0.5 ± 0.8	0.5 ± 0.7	0.95[b]	$R^2 = 0.00$; $p = 0.41$	$R^2 = 0.02$; $p = 0.25$
rate of climb (m s^{-1})	0.87 ± 1.3	0.87 ± 1.2	0.99[b]	$R^2 = 0.00$; $p = 0.43$	$R^2 = 0.00$; $p = 0.32$
ΔU_{grnd} (m s^{-1})	−0.88 ± 1.8	0.5 ± 2.6	0.06[b]	$R^2 = 0.00$; $p = 0.63$	$R^2 = 0.47$; $p = 0.001$
ΔU_{air} (m s^{-1})	−0.03 ± 1.9	1.0 ± 2.8	0.10[b]	$R^2 = 0.00$; $p = 0.45$	$R^2 = 0.47$; $p = 0.001$
ΔPE (J)	0.08 ± 0.13	0.08 ± 0.11	0.95[c]	$R^2 = 0.00$; $p = 0.41$	$R^2 = 0.02$; $p = 0.25$
ΔKE_{grnd} (J)	−0.12 ± 0.25	0.14 ± 0.46	0.08[c]	$R^2 = 0.00$; $p = 0.71$	$R^2 = 0.46$; $p = 0.001$
ΔKE_{air} (J)	−0.05 ± 0.24	0.23 ± 0.56	0.25[c]	$R^2 = 0.00$; $p = 0.30$	$R^2 = 0.47$; $p = 0.001$
ΔTE_{grnd} (J)	−0.04 ± 0.21	0.22 ± 0.47	0.06[c]	$R^2 = 0.00$; $p = 0.33$	$R^2 = 0.54$; $p = 0.001$
ΔTE_{air} (J)	0.03 ± 0.21	0.35 ± 0.58	0.11[c]	$R^2 = 0.00$; $p = 0.50$	$R^2 = 0.51$; $p = 0.001$
WBF (Hz)	7.1 ± 2.7	6.2 ± 4.4	0.44[b]	$R^2 = 0.27$; $p = 0.01$	$R^2 = 0.00$; $p = 0.82$
peak (g)	4.8 ± 1.5	3.9 ± 1.1	0.03[b]	$R^2 = 0.00$; $p = 0.64$	$R^2 = 0.02$; $p = 0.25$
mean (g)	3.6 ± 1.3	3.0 ± 1.0	0.12[b]	$R^2 = 0.00$; $p = 0.95$	$R^2 = 0.00$; $p = 0.32$

[a]ANOVA (regression).
[b]*t*-test.
[c]Mann–Whitney *U*-test.

presumably involved with foraging (no interactions between birds were recorded), a few ($n = 7$) were directly involved in prey capture, as evidenced by neck extension or visible prey (see next section). Overall, segment 2 flight speeds in the turns were slightly, but significantly, slower than average coursing speed (mean $U_{grnd} = 8.6 \pm 1.5$ m s^{-1} versus 9.7 ± 1.6 m s^{-1}; *T*-test $p = 0.006$; range: 12.8–5.4 m s^{-1}; U_{air} 9.0 ± 2.1 m s^{-1} versus 9.8 ± 1.9 m s^{-1}; *U*-test $p = 0.03$; range: 14.7–6.0 m s^{-1}; electronic supplementary material, table S3).

When examining the dynamics within individual turns with respect to wind direction, we could detect no statistically significant difference in the mean change in U_{grnd} (or KE_{grnd}), U_{air} (or KE_{air}) or height (PE) in downwind versus upwind flights (table 5). Further, we found no statistically significant trends in the change in *U*, KE or PE with wind speed for downwind turns (figure 4*a–c*). However, birds turning into the wind exhibited marked increases in flight speed, KE and TE with increasing wind speed (e.g. U_{grnd} $R^2 = 0.47$, $p < 0.001$; KE_{grnd} $R^2 = 0.46$, $p = 0.001$; figure 2; figure 4*a–c*, respectively, and table 5). On average, birds turning into the wind tended to increase their TE in both the ground and air reference frames more than those turning downwind; however, due to the large variances (as a function of wind speed) the differences were not statistically significant (e.g. mean $\Delta TE_{grnd} = -0.04 \pm 0.21$ J downwind versus $\Delta TE_{grnd} = 0.22 \pm 0.47$ J upwind; $p = 0.06$; and $\Delta TE_{air} = 0.03 \pm 0.21$ J downwind versus $\Delta TE_{air} = 0.35 \pm 0.58$ J upwind; $p = 0.11$; table 5)

WBF during turns was not statistically different between downwind and upwind turns (downwind 7.1 ± 2.7 Hz versus upwind 6.2 ± 4.4 Hz; $p = 0.44$). However, a significant positive correlation between WBF and wind speed existed for birds turning downwind, suggesting an increase in WBF to regain airspeed lost in the downwind turn (table 5). A significant decrease in WBF, due to an increase in the use of intermittent non-flapping postures (glides and partial bounds), was observed with an increase in angular acceleration (g) ($R^2 = 0.10$; $p = 0.02$; figure 5). The average WBF of the tagged birds upon their release, where they presumably exhibited maximum power, was significantly higher than their WBF while foraging (14.3 Hz versus 6.0 Hz (straight) versus 7.9 Hz (turning); figure 5, inset). The birds only rarely gave up flapping for an entire segment of manoeuvering (i.e. WBF = 0). Expressed as a percentage of segments before, during and after turns, respectively, persistent intrinsic (non-flapping) manoeuvers were 2.3%, 7.9% and 9.7% of the sample.

As our categorizations and broad statistical characterization have obscured some of physical causalities of the individual turning flights, four of these flights are described in individual detail in electronic supplementary material, figures S1–S3. Of particular note is that some of these birds increase energy through the upwind turns without flapping (see, in particular, electronic supplementary material, figure S1), indicating the exploitation of near-ground velocity gradients. However, it is also the case that increases in PE and KE also probably result from flapping.

(c) Dynamics of prey capture

We recorded three instances where the swallow and its prey were both visible. Owing to the small number of events and because the larger insects seen by the cameras are probably not representative of typical barn swallow prey, we performed no statistical analysis of these events. However, a descriptive account of the dynamics and videos showing the events is provided in electronic supplementary material, S5–S9.

4. Discussion

(a) Facultative versus intrinsic manoeuvering

Our results revealed that flapping (facultative) manoeuvering was the dominant characteristic of the flight repertoire of barn swallows. Brief, intermittent non-flapping phases

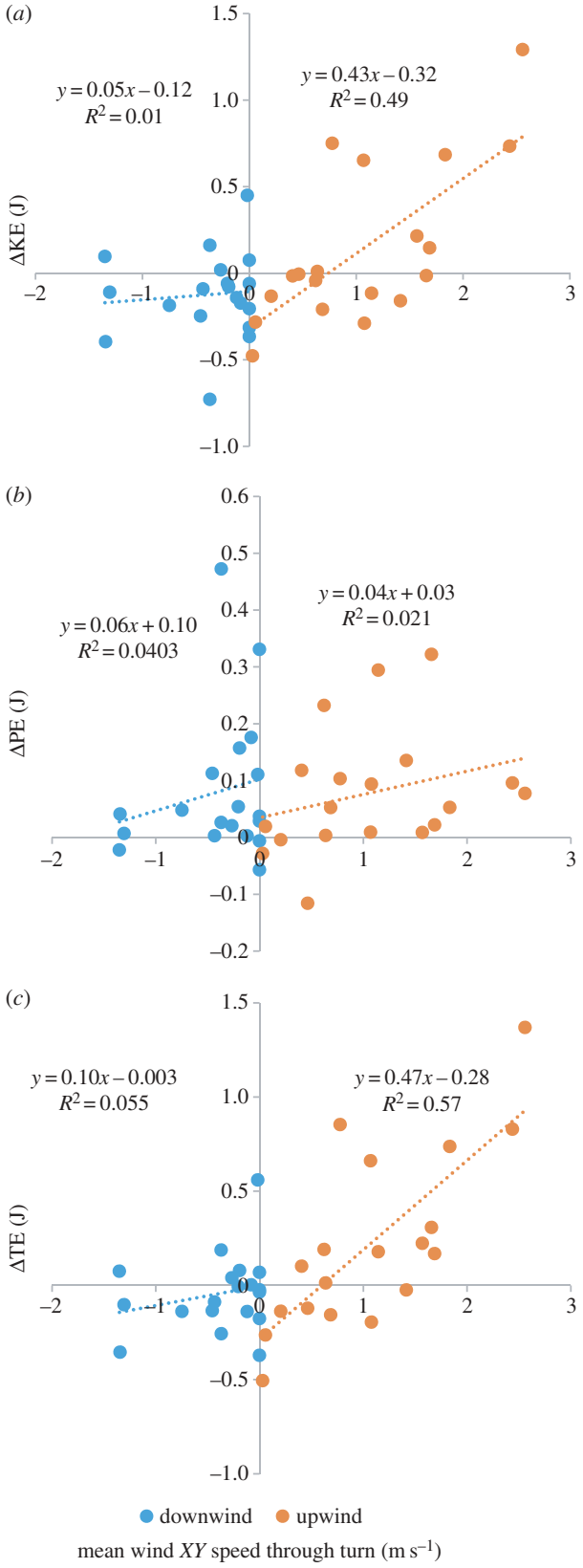

Figure 4. Change in energy during turns during flight in barn swallows. (*a*) Kinetic energy KE_{grnd} during turns. Birds turning into the wind gained ground-speed (*XYZ* coordinate space) and kinetic energy in that reference frame (ANOVA linear regression $R^2 = 46$; $p = 0.001$); trend was not evident downwind ($p = 0.71$). (*b*) Change in potential energy (PE) (upwind regression ANOVA, $p = 0.25$; downwind regression ANOVA, $p = 0.41$; blue points). (*c*) Change in TE (PE + KE_{grnd}) during turns. Birds turning into the wind gained energy (ANOVA, $p = 0.001$) but not downwind ($p = 0.33$). Energy was calculated using bird ground speed, and an average mass of 0.0166 kg. Upwind energy gain probably results from dynamic soaring (electronic supplementary material, figure S1), as well as wing flapping.

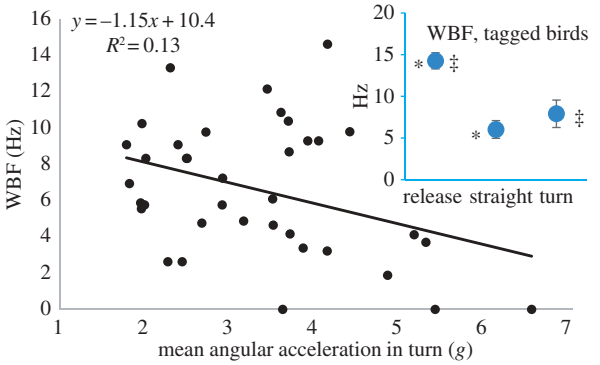

Figure 5. Change in wingbeat frequency (WBF) as function of angular acceleration during turns. (ANOVA, $p = 0.02$) Inset: mean WBF (paired *t*-tests) of tagged individuals ($n = 4$) during release, straight foraging, and ($n = 3$) turning foraging flights. $^{‡}p = 0.051$; $^{*}p = 0.003$.

contributed to significant variation in time-averaged WBF, but less than 10% of flight segments consistent solely of a non-flapping (intrinsic) manoeuver. This, coupled with similar observations from cliff swallows engaged in tandem flight [20] suggests that flapping dynamics should to be incorporated into existing ecomorphological models of manoeuvering capacity [23,24]. However, further comparative study similar to our present effort is necessary for the construction of new models.

Relevant to the question of fixed-wing assumptions in manoeuvering flight is to what degree the anatomical and physiological stress of high-*g* manoeuvering affects the swallows' behavioural choices. Reduction in WBF with increasing angular acceleration (figure 5) may be a result of both the need to present a full-wing area to maximize lift, as well as a reluctance to subject the pectoralis and structural components of the wing to the additional accelerations of flapping.

The high ground speeds (U_{grnd}) of barn swallows reported here and elsewhere [14,17] have been hypothesized to result from the need to maximize their foraging area at minimum cost, and allow them to encounter and overtake ground-associated prey at a high rate before those prey, which may be highly manoeuverable themselves, can return to the safety of the ground [14]. Moreover, high airspeeds increase the swallows' intrinsic agility by quickly making available the high force asymmetries needed for rolling manoeuvers. Flying at high airspeeds also increases the efficacy of the tail in controlling rolling manoeuvers by countering adverse yaw [36,37]. The relative invariability in airspeed through these routine manoeuvers suggests that the barn swallows make every effort to preserve kinetic energy; that is, they generally avoid slowing into the expensive facultative manoeuvering realm, which would increase their induced power cost (e.g. [25]), and thus decrease their foraging efficiency both through increased cost and possibly decreased success. Further, our results suggest that swallows will produce small radius, high *g* turns, which are also expected to incur large induced drag costs, only when motivated by immediate energy reward in the form of prey (e.g. electronic supplementary material, figure 2*d*).

While the high-aspect ratio wings of swallows [14] should help to minimize induced drag costs, particularly when using high angles of attack typically employed during manoeuvering, maintaining U_{air} inevitably involves imparting energy to the environment in the form of flapping. However, the ability to exploit the steep, although intrinsically narrow (1–3 m s^{-1}), near-ground wind gradients without continuous flapping may

be of substantial energetic importance to these animals. Consequently, the wind gradients in which barn swallows forage are likely to be a significant selective pressure for the evolution of low wing loading in these and other insect-foraging avian species and bats [23,24]. A future test of this hypothesis might come in the form of ecomorphological contrasts between swallows and small insectivorous bats that forage at times of lower wind energy at night. Whatever the evolutionary impetus, given their liability in terms of mass-specific power production and low-speed performance [14], the large wings (and tails) of barn swallows are clearly better tuned to high-speed, fixed-wing flight than other passerines, or even other swallows (e.g. cliff swallows). Notably, the average WBF of foraging tagged swallows was approximately half of what they exhibited during escape flight (figure 5, inset), suggesting that they hold considerable flapping power in reserve when foraging, and may use that power during more protracted vertical prey capture manoeuvers similar to those employed by cliff swallows (D. R. Warrick, unpublished data, 1997). Future studies that provide more detailed kinematics than we are able to achieve here will be required to discern the relative importance of fixed-wing (intrinsic) versus flapping flight (facultative) manoeuvering to these and other swallow species.

(b) Exploitation of the shear layer

Exploitation of the near-ground wind gradient by barn swallows during foraging (figure 2*a*) is a heretofore unappreciated feature of their aeroecology, although it cannot be unexpected. Given their predilection for gliding, low-altitude flight and possession of an exceptionally low wing loading (contrary to popular belief [38,39]), 2.5 times lower than even the most lightly wing-loaded seabird, the frigatebird (*Fregata magnificens* [40]), barn swallows would seem to be well suited to take advantage of this energy. This same flight morphology would also allow them to take advantage of gust soaring—that is, increasing altitude and potential energy with a sudden increase in incident air velocity [41]. Unfortunately, we cannot test for this effect with the techniques described here, and addressing this hypothesis must wait for the development of anemometers small enough to be carried by swallows.

Whatever the precise mechanism for extracting energy from the wind, we can only speculate upon the impact on the daily energy budget, evolution and biogeography of barn swallows. We note that there is a significant correlation of increasing flight speed and energy with increasing wind speed when birds turn into the wind (figure 4*a–c*), but without including the energy the bird itself may provide, we cannot reasonably estimate the biological significance of the phenomenon, nor can we completely discount the possibility that vagaries in wind velocity affected our interpretation of these very brief events. However, we can examine the circumstances of some of those flights to illustrate the potential for extracting energy from this aerial environment (figure 1*b*; electronic supplementary material, figures S1 and S2*a–d*). For example, BS-04 (figure 1*b*; electronic supplementary material, figure S1), turned using a continuous glide during a 6 *g* turn and gained approximately 0.73 J in a single, half-second turn through a relative small 0.5 m gradient of approximately 3 m s^{-1} wind. Likewise, BS-42 gained over 1.37 J with the investment of two seemingly shallow wingbeats (electronic supplementary material, figure S2*b*), although some of the increase in KE_{grnd} came from the bird turning away from an initial direct headwind early in the turn, resulting in higher U_{grnd} in the turn (the only instance that we observed of this phenomenon, electronic supplementary material, figure S2*b*). By contrast, although BS-59 turned into the wind in a probable prey capture manoeuver (electronic supplementary material, figure S2*d*), no height was gained, and the small radius turn occurred below the extrapolated $U_z = 0$ height. As a result, the bird lost significant U_{grnd} and KE (−0.51 J). That the barn swallows tended to increase their TE when turning into the wind—whether by flapping harder, and/or capturing energy from the near-ground wind gradient is, at least, evidence that the birds were aware of the wind speed and direction and altered their behaviour in reference to it. These flight patterns may also reflect that, when turning into the wind, the swallows increased their own energy input to maintain the desired foraging speed over ground; whereas, for swallows simply interested in changing directions, climbing up through the velocity gradient was a convenient means by which to reduce the cost of foraging.

In late June on the Oregon coast, barn swallows were feeding chicks and foraging nearly continuously from dawn to dusk, over a 15 h period of time. Without new technology, the number of turns of any type that a swallow makes in a day will remain unknown, but even a conservative assumption of a 0.25 J gain once per minute yields 225 J of energy saved per day. Over the course of a month, this would amount to the energy invested in one barn swallow egg (4.2 kJ per gram egg mass [42]; barn swallow eggs approximately 1.9 g [43]). While seemingly a modest savings, it should be noted that the winds on the Oregon coast typically offer far more energy than the days that were sampled, with (24 h) wind speed averaging 6 m s^{-1} during the breeding season [44], and diurnal wind speeds frequently exceeding 12 m s^{-1} (D. R. Warrick, personal observation, 1983–2016) How barn swallows alter their behaviour *vis à vis* this and other greater energy environments, and how such environments may have shaped the evolution of local populations are unstudied, but there is evidence that variation in available wind energy has affected the distribution of other dynamic soarers. Suryan [45] cogently describes trends among species of albatross, noting that lower wing-loaded species inhabit regions with lower wind and wave energies, whereas albatross species with higher wing loading typically forage overseas with greater winds. If exploiting wind energy during foraging, at this much smaller spatial scale, is a significant component of the energy budget of swallows, such a strategy predicts that there may exist differences in wing loading among populations that inhabit areas of greatly different wind energy. Moreover, variability within a habitat may, as it does for dynamically soaring seabirds, influence foraging strategy (e.g. choosing not to forage, or only foraging at higher altitude at times of low wind [46]) or foraging tactics (e.g. preferentially turning into the wind [3,11]).

Swallows may also react to turbulence, the variability in wind velocity at different length and temporal scales. Our measurements of turbulence intensities ranging from 17 to 42% were similar to intensities reported for other studies near the ground (approx. 30%, summarized in [33]). The observed length scales of the turbulence in the horizontal plane were 5–13× longer than the wingspan of the barn swallows, so we interpret that swallows would have perceived the horizontal turbulence more as persistent wind speed rather than as

disruptive gusts that would have perturbed them by inducing roll. We estimate the swallows did not perceive the turbulence in the vertical direction as it was of relatively lower magnitude, and it was at length scale 48× shorter than their wingspan. Further, their relatively fast air speeds (U_{air}) would reduce the perceived intensity of the turbulence [33].

In all, it is important to recognize that the barn swallow's version of this type of flight is considerably more complex than that of seabirds. While an albatross can move with relative impunity through its obstruction-free environment, needing only to manipulate wind gradients to minimize its cost of transport, swallows must simultaneously manoeuver to catch evasive prey, avoid obstacles and position themselves, more often than not, to make positive use of the energy of the air. No doubt there exists a formidable learning curve for young swallows foraging at the edge of the world.

Ethics. All procedures were approved by the Institutional Animal Care and Use Committees of the University of Oregon and the University of Montana. Animal capture, tagging and release were conducted under scientific collecting permits from the US Fish and Wildlife Service and the Oregon Department of Fish and Wildlife.

Data accessibility. The [X, Y, Z] coordinate data for the barn swallow flights analysed here, together with the corresponding wind speed data, can be accessed on Dryad (doi:10.5061/dryad.4v5r8).

Competing interests. The authors declare no competing interests.

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